

CONTRIBUTIONS TOWARD A CLASSIFICATION  
OF MODERN ISOSPONDYLOUS FISHES

BY

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# CONTRIBUTIONS TOWARD A CLASSIFICATION OF MODERN ISOSPONDYLOUS FISHES

By WILLIAM A. GOSLINE

THAT the classification of the modern isospondylous fishes (Order Clupeiformes) is unsatisfactory would be admitted by all who have worked with them. The present contributions to the subject are divided into four sections. The first traces one structural complex, the caudal skeleton, through the whole group. The second and third have to do with controversial sections of isospondylous classification. In the final section a revised arrangement of modern forms, down to superfamily, is presented and its rationale discussed. The sections are in logical sequence, but it may also be noted that they are arranged in order of descending assurance on the part of the author. More, perhaps, than usual with classifications, that presented in section four is merely a "progress report".

Regarding nomenclature, the ordinal, subordinal, and superfamily names are formed according to the system proposed by Berg (1940:353). The following procedures concerning common names have been adopted. Where an old literature name is well known it will be used. Thus the members of the order Clupeiformes will be called the isospondylous fishes, and those of the suborder Esocoidei the haplous fishes. Where a common name in this paper ends in *oid*, it refers to a member of a suborder. For example, the term salmonoid fishes will be used to designate all of the forms of the Suborder Salmonoidei and not just those of the superfamily Salmonoidae. No common names will be used for superfamily<sup>1</sup>.

Bone nomenclature is that of Devillers (1958).

The work on which this paper is based was nearly all done at the British Museum (Natural History) and I wish to thank the members of the fish division of that Museum for the facilities extended me and for permission to examine the skeleton and fish collection. I also wish to thank them, notably N. B. Marshall, for the discussion and suggestion of various points incorporated into the paper. The following individuals have been kind enough to read part or all of the manuscript and to offer constructive criticism: E. H. Ahlstrom, H. B. Bigelow, D. M. Cohen, D. H. Dunkle, N. B. Marshall, and G. W. Mead. Finally, I am greatly obligated to the John Simon Guggenheim Foundation for the fellowship that has made this work possible.

<sup>1</sup> If Berg's termination *oidi* is used for suborder, the problem of devising different common names for subordinal and superfamily categories is equally great whether the superfamily ending *oidae*, recommended by the London Colloquium, or Berg's *oidae* is used.

SECTION 1. THE CAUDAL SKELETON OF  
MODERN ISOSPONDYLOUS FISHES

## INTRODUCTION

The caudal skeleton of teleostean fishes has been the subject of papers by Barrington (1937), Blanco (1935), Hollister (1936, etc.), Kölliker (1860), Lotz (1864), Regan (1910*a* and *b*), Totton (1914), Whitehouse (1910*a* and *b*, 1918), and others. Nevertheless, the accumulated information is rather amorphous, and the caudal skeleton is usually either ignored or briefly dismissed in taxonomic papers. A large part of the difficulty would seem to stem from the failure to establish stable reference points as a basis for comparing one caudal skeleton with another: hence the introductory remarks that follow.

In a relatively simple caudal skeleton like that of *Amia* (Goodrich, 1909, fig. 311 or Whitehouse, 1910*a*, fig. 5), each of the last several vertebrae articulates with the base of a single caudal ray by means of a *hypural* (which is probably a hemal spine fused with the radial element of the fin ray, cf., Totton, 1914:255). In the teleostean fishes, however, complications of several types occur. In the first place, several of the posteriormost vertebral centra disappear (see below). Second, the hypural elements themselves become reduced in number, presumably through loss and fusion, so that in teleosts there are usually two to several caudal rays articulating with each hypural. Third, one or more elements of the caudal skeleton above the vertebral column lose their proximal contact with the neural arches (this is also true of *Amia*) becoming the so-called *epurals*. Finally, in the more primitive isospondylous fishes there are one to four pairs of bones that lie along the posterior end of the spinal cord; these are the *uroneurals*.

A final term, *urostyle*, has been used in the literature to cover such a wide variety of structures that it will be completely avoided here. Supposedly the urostyle represents the last upturned vertebral centra. However, Regan (1910*a*) and Ramanujam (1929) have shown that the so-called urostyle of the Clupeidae is mostly formed of uroneurals (see footnote 2 of the present paper), and the uroneurals may form a large part of the "urostyle" of at least some higher teleosts.

Another difficulty lies in the fact that at least two of the centra at the end of the vertebral column in such a fish as *Elops* disappear as separate entities in the higher teleosts. Thus the last visible centrum of one fish is not always the homologue of the last centrum of another. To get around this difficulty it is necessary to establish some reference point that is both homologous and identifiable in as many teleosts as possible. The most satisfactory seems to be the posteriormost vertebra that is consistently present in all isospondylous fishes (except for such aberrant forms as *Coilia*) and is usually present in other teleosts; this is here termed the *terminal vertebra* (TV of Text-figs. 1-15). It can usually be identified by a series of criteria (though the misimpression should not be given that any or all of these will easily or even securely establish the terminal vertebra of all fishes). The best single feature is probably the nature of the anteriormost hypural articulating or fused with it.

In most lower teleosts (and indeed in many percoids) the hypurals to the lower caudal lobe are quite constant in number (three) and general shape. The uppermost

of these (HY<sub>3</sub> of Text-figs.) is a rather narrow strut that is never expanded posteriorly. The next hypural below (HY<sub>2</sub> of Text-figs.) is broadly wedge-shaped, i.e., considerably expanded toward the rear. Below this again is another strut-like hypural with a broad basal articulation or area of fusion with a centrum; throughout the paper this will be considered the lowermost hypural (HY<sub>1</sub> of Text-figs.), and the vertebra with which it articulates is the terminal vertebra. This hypural, or *hypural 1*, almost always differs from those behind and above it in having on each side near its base a lateral flange, which usually terminates posterolaterally in a sharp point. (This flange serves for the attachment of part of the flexor caudalis ventralis superficialis muscle (Greene and Greene, 1914: 46) and probably in part as protection for the blood vessels that exit from the vertebral column behind the base of hypural 1. In these respects hypural 1 is the terminal structure retaining a number of hemal arch characteristics.) Generally, the terminal vertebra may also be identified in other ways. Whatever its relationship with centra (if present) behind it, there is always a normal, hourglass-shaped centrum and a typical intervertebral articulation immediately in front of it. More diagnostic perhaps is that if the front pair of uroneurals wedge into or fuse with any centrum, it is that of the terminal vertebra (except apparently in osteoglossoids).

In some recent teleosts one or two separately ossified centra may remain visible in the adult; if so these are here termed *postterminal*<sup>1</sup> centra (PT of Text-figs. 1-4, 6, 7, 10 and 13-15) and are numbered from front to rear. When there are two post-terminal centra, hypural 1 alone articulates or fuses with the terminal vertebra, and hypurals 2 and 3 arise together on the first postterminal centrum (as in Text-figs. 1-4).

Vertebrae just anterior to the terminal vertebra are here called *preterminal vertebrae* (PR of Text-figs.) and are numbered from back to front.

The structure of the upper half of the caudal skeleton seems to be more subject to variation than the lower. This is perhaps to be expected as there is phylogenetically a progressive retraction of the vertebral column from the upper caudal lobe. At any rate, in the isospondylous fishes there is some fluctuation, from specimen to specimen as well as from species to species, in the number of uroneurals and epurals, and from genus to genus in the number of upper hypurals.

Two other types of ontogenetic and individual variation should be mentioned. One is the abnormal but frequent doubling of the neural or hemal arches attached to any one centrum, even the terminal centrum (Totton, 1914: 253). The other is the nature of the association between these arches and their centra. In young fishes the neural and hemal arches are wedged into their centra and only later in ontogeny do they fuse with them; however, in some forms, e.g., *Albula*, such fusion never does take place.

Finally, it should be noted that dried skeletons, which have been used here, show especially the superficial features of the bones whereas stained and cleared specimens show more of the deeper features. Furthermore, for practical reasons

<sup>1</sup> Dr. E. H. Ahlstrom informs me that he prefers to retain the term *urostyle* for those centra with which the hypurals articulate. If the confusion that has arisen from including the uroneurals in the "urostyle" can be cleared away, there is much to be said for this, especially in view of the term "post-terminal centra" with its self-contradictory adjective that is used in this paper.

dried skeletons are usually prepared from large adults whereas stained and cleared specimens are preferably small. Thus an investigation based on dried material is likely to emphasize one set of caudal features, that based on cleared specimens another.

#### COMPARATIVE CAUDAL MORPHOLOGY

In the following accounts of individual caudal skeletons, a basal group (Diagram 1) is dealt with first. The "lineages" of caudal structure presumably arising from these basal forms are then discussed. Finally the component members of these

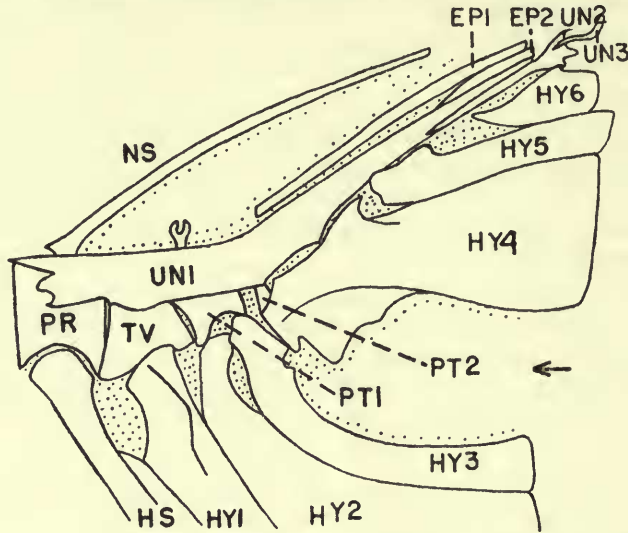


FIG. 1. Caudal skeleton of *Alepocephalus rostratus*,  $\times 5\frac{1}{3}$ . Stippling indicates interosseous or infraosseous areas. The arrow indicates the midpoint between the lobes of the caudal fin. EP, epural (these are numbered from top to bottom); HS, hemal arch and spine; HY, hypural (hypurals are numbered from bottom to top; hypural 1 is really in large part the hemal arch and spine of the terminal vertebra); NA, neural arch (only); NS, neural arch and spine; PR, preterminal vertebra (these are numbered from rear to front); PT, postterminal centrum (these are numbered from front to rear); TV, terminal vertebra; and UN, uroneural (these are numbered from front to rear).

"lineages" are taken up. Superfamily and subordinal names are those adopted in Section 4 of this paper; for the moment it need only be noted that *Chanos*, *Kneria*, *Phractolaemus* and *Cromeria* are here included in the Gonorhynchoidei. Failure to mention certain families is due to lack of available material.

Of the caudal skeletons examined the following would seem to be among the most primitive<sup>1</sup>: *Elops* (Hollister, 1936, fig. 14), *Alepocephalus* (Text-fig. 1), *Salvelinus* (Text-fig. 2), *Esox* (Text-fig. 3), and *Hiodon* (Text-fig. 4). All of these have a number

<sup>1</sup> Underlying the use of the terms "unspecialized" and "primitive" throughout this paper is the assumption that in teleostean fishes there has been a progressive fusion and loss of parts in the evolution of the caudal skeleton. (According to this concept the most highly simplified caudal skeletons are often the most "advanced" whereas the more complex are frequently the most "primitive".)

of unspecialized<sup>1</sup> features in common: the front end of the anterior uroneural overlaps, but neither wedges deeply into nor fuses with, the terminal vertebra; hypural 1 is the only hypural articulating or fusing with the terminal vertebra;

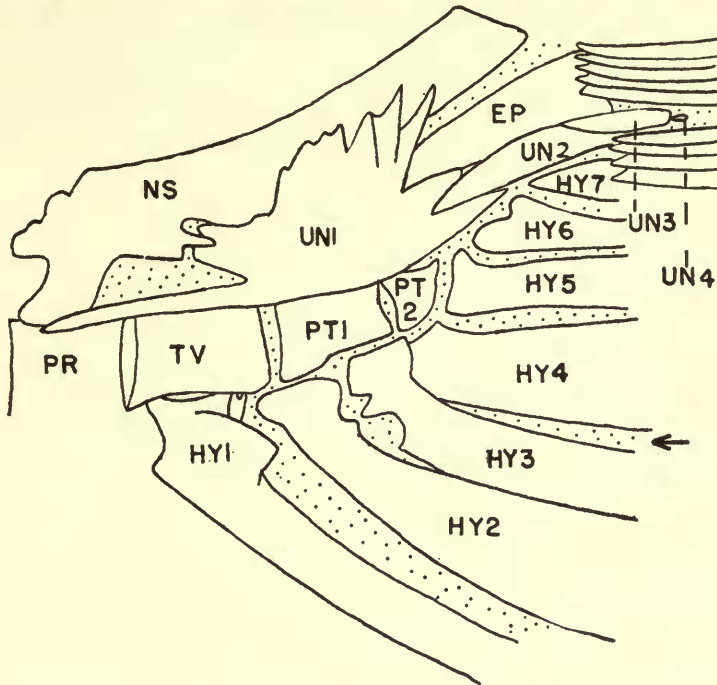


FIG. 2. Caudal skeleton of *Salvelinus grayi*,  $\times 6\frac{2}{3}$ . Bases of some of the upper fin rays are included to show gap for posterior uroneurals.

hypurals 2 and 3, and these only, articulate with the first postterminal centrum; and a portion of a second postterminal centrum is always visible.

From the type of caudal skeleton represented in these primitive forms the more specialized caudal structures found among isospondylous fishes have presumably arisen. Indeed it seems possible to trace in the caudal skeleton four main "lineages" (I-IV of Diagram 1), as will be done here. As to these, *Elops* and *Alepocephalus*

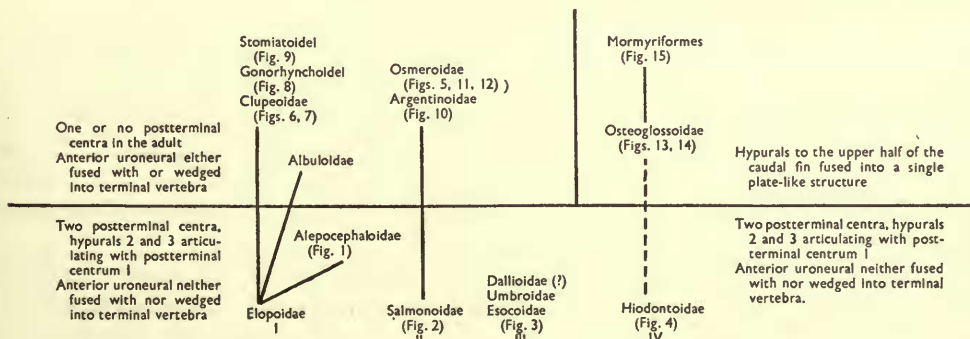


Diagram 1

are considered to be basal members of a stock including the suborders Elopoidei, Clupeoidei, Gonorhynchoidei, and Stomiatoidei; *Salvelinus* represents the Salmonoidei; *Esox*, the Esocoidei; and *Hiodon*, the Osteoglossoidei and Mormyriiformes.

Of these four presumed lineages, the caudal skeletons of adult members of the Salmonoidei (II) are, with the exception of those of the Salangidae and of the neotenic aplochitonid *Lovettia*, the most easily recognizable. In this suborder the last few preterminal vertebrae have neural and hemal spines with flattened, anteroposteriorly oriented blades (Text-fig. 5). These together tend to make up a flange or keel running

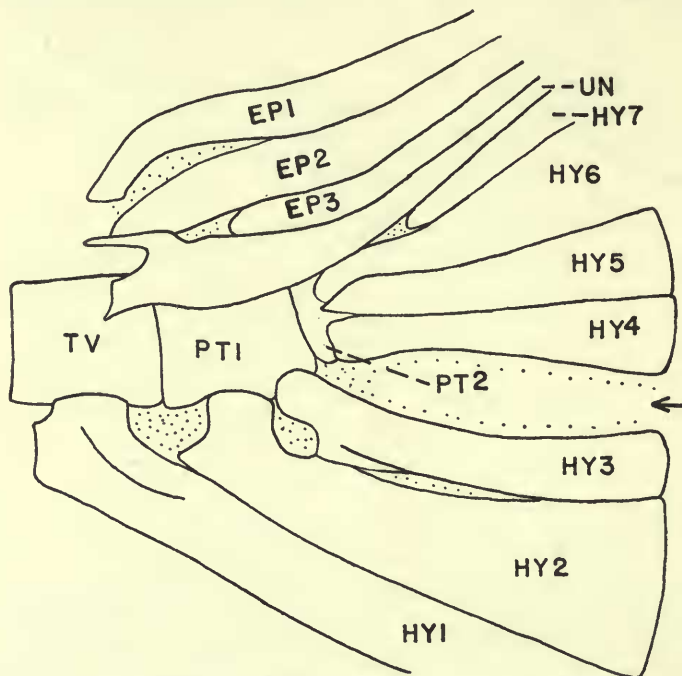


FIG. 3. Caudal skeleton of *Esox lucius*,  $\times 2\frac{2}{3}$ .

above and below the posteriormost portion of the vertebral column. This structure is developed to a variable degree in the different salmonoid fishes but is only totally absent in *Lovettia* and the salangids; it is not found in the members of any of the other lineages, though *Albula* approaches it. In addition there is a series of about 10 small, more or less s-shaped accessory (procurrent) rays in front of the caudal fin above and below in the salmonoids including *Lovettia* and the salangids; these salmonoid accessory rays are easier to recognize than they are to differentiate from those that occur in many other isospondylous fishes.

The osteoglossoid-mormyriiform lineage (IV) has two quite different types of caudal skeleton, the one represented by *Hiodon* (Text-fig. 4) and the other by *Osteoglossum* (Text-fig. 13), *Heterotis* (Text-fig. 14), and *Mormyrus* (Text-fig. 15). It would be difficult to confuse the second type with any other isospondylous caudal



skeleton, but it is quite possible that *Hiodon*, by a different route, may have produced a fish with a caudal skeleton similar to that in the clupeoid stock. The main caudal feature militating against a hiodontid derivation for such a fish as *Gonorhynchus* is that this genus and the great majority of the other fishes here assigned to Lineage I have 17 branched caudal rays, whereas all of the members of the osteoglossoid-mormyriiform lineage including *Hiodon* have 16 or fewer branched caudal rays.

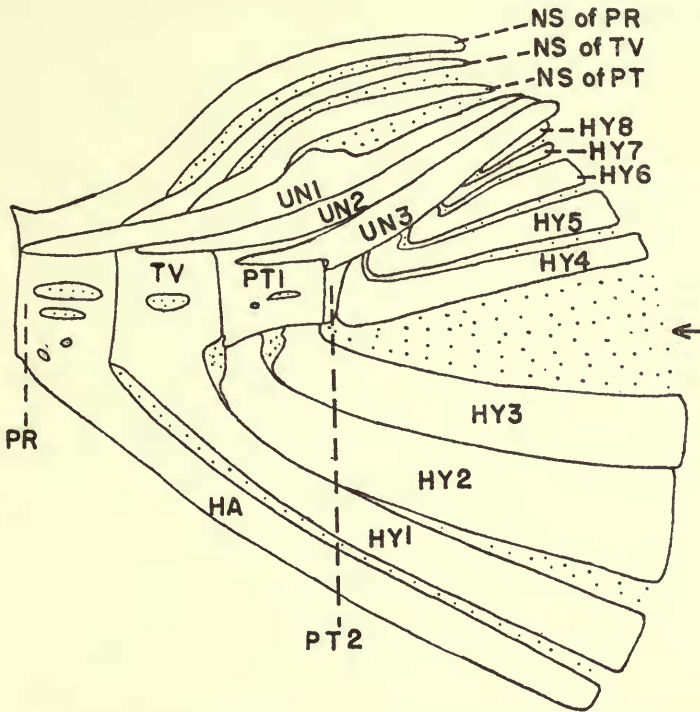


FIG. 4. Caudal skeleton of *Hiodon alosoides*,  $\times 4\frac{2}{3}$ . In this fish the preterminal and terminal vertebrae and the first postterminal centrum each have a neural arch and spine that articulates with its centrum between the lateral unoneurals of the two sides.

The haplomous lineage (III), as here understood, contains only the Esocidae, Dalliidae, and Umbridae. Chapman's (1944) assignment of the southern hemisphere aplochitonids, retropinnids, and galaxiids to the haplomous fishes is not accepted partly because of the caudal skeleton but also for other reasons that will be developed in Section 2 of this paper. The caudal skeletons of *Esox* (Text-fig. 3), *Umbra* and *Novumbra* are very similar and primitive. No caudal skeleton of *Dallia* has been available for investigation.

The final lineage recognized here is that including the clupeoids and various other groups (I). About the only feature held in common by all its members is the high number (17 except in *Coilia*, *Phractolaemus*, and *Cromeria*) of branched rays in the caudal. This would seem to distinguish them from the osteoglossoid stock.

The absence of antero-posteriorly directed flanges on the last few neural and hemal spines would in turn separate them from the salmonoids. Nevertheless, Lineage I as accepted here may prove to be a heterogeneous assemblage. For example, such groups as the Gonorhynchoidei and Stomiatoidei may very possibly have arrived at caudal skeletons similar to those of the Clupeoidae by a process of parallel or convergent evolution rather than because of genetic relationship: about all that can be said for these questionable groups is that their caudal skeletons do not seem to show relationships with the salmonoid, esocoid, or osteoglossoid lineages.

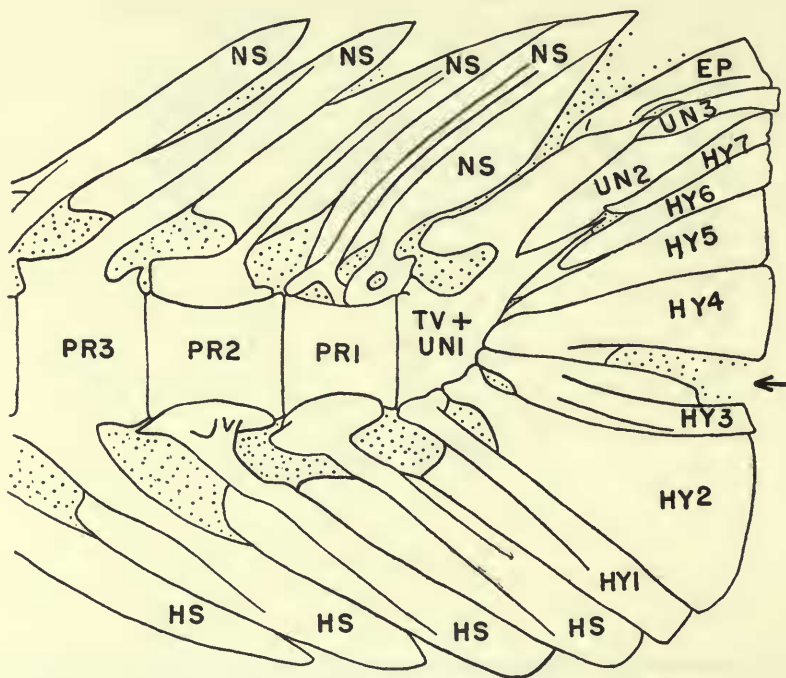


FIG. 5. Caudal skeleton of *Hypomesus olidus*,  $\times 10\frac{2}{3}$ .

*Suborder Elopoidei.* Caudal skeletons of *Elops*, *Megalops*, *Albula* and *Pterothrissus* have been examined. All except the last have been discussed and figured by Hollister (1936, figs. 14-39). Though all are primitive, there is considerable difference between *Elops* and *Megalops* on the one hand and *Albula* and *Pterothrissus* on the other. In *Elops* and *Megalops* there are four pairs of uroneurals overlapping one another rather in the fashion of the body scales; in the adult *Albula* and in *Pterothrissus* there are only two pairs of uroneurals and these are arranged almost linearly, one pair behind the other. In *Elops* and *Megalops* the terminal vertebra bears a neural arch and behind it lies a small median crest above and between the uroneurals of each side; in *Albula* and *Pterothrissus* the terminal vertebra bears no neural arch and the median crest behind it has greatly expanded.

All of the species of Elopoidei appear to have 17 branched rays. *Elops* and *Albula*, but not *Pterothrissus* and *Megalops*, have a single bony fulcral plate at the front of the caudal base above and below.

*Superfamily Alepocephaloidea*. The caudal skeleton of *Alepocephalus* (Text-fig. 1) shows a peculiar combination of primitive (see above) and specialized features. There are the usual 17 branched caudal rays. Only one of the uroneurals is elongated, but this reaches forward to cover part of the first preterminal vertebra. Parts of two postterminal centra are visible, and hypurals 2 and 3 articulate with the first of these. Of specializations, the most notable perhaps is the long, curved, rod-like form of the upper epural and of the posterior neural spine.

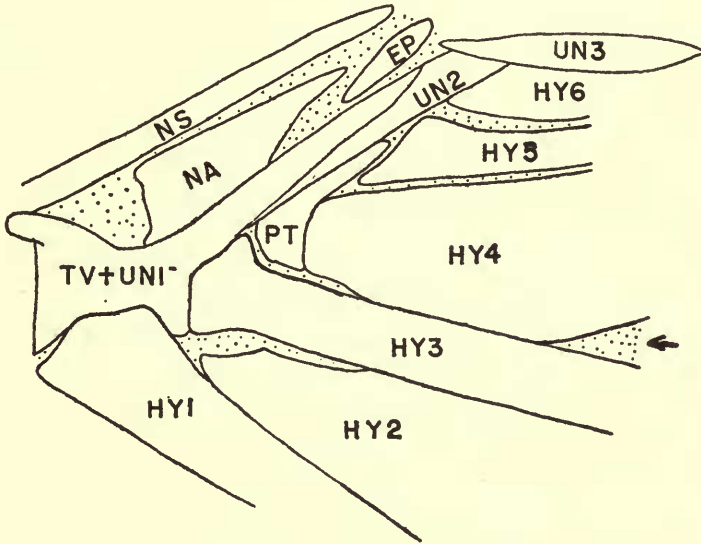


FIG. 6. Caudal skeleton of *Chirocentrus dorab*,  $\times 4\frac{2}{3}$ .

*Superfamily Clupeoidea*. The caudal skeleton of *Chirocentrus* illustrated here (Text-fig. 6) differs from that of the other clupeids and engraulids examined (aside from *Coilia*) only in the somewhat enlarged and long-based neural arch on the terminal vertebra and the very slight development of a lateral spine on hypural 1 (cf., Text-fig. 7). A specimen of *Nematolosa* examined, and illustrations of *Clupea* given by Ramanujam (1929, fig. 27) and of *Anchoviella*, *Harengula*, *Opisthonema*, and *Sardinella* by Hollister (1936, figs. 45-53) agree with *Chirocentrus* in all basic features. In these fishes the anterior uroneural is fused proximally with the terminal vertebra; hypural 2 has no basal articulation; one postterminal centrum is visible; and the neural arch of the terminal vertebra has a dorsally projecting flange that is usually higher than broad.

Many of these features have been developed in other isospondylous fishes but the loss of a basal articulation for hypural 2 apparently occurs only in portions of Lineage I. Normally, hypurals 2 and 3 articulate close together on a single centrum;

if two postterminal centra are present hypurals 2 and 3 articulate with the first, which would consequently indicate that when two postterminal centra are present the first is of double origin. In the herring, however, Ramanujam (1929) has shown by embryological investigation that it is the terminal centrum that is of double origin (it seems to be formed by the fusion of the terminal vertebra with the front half of the first postterminal centrum), and that presumably with this change hypural 2 has lost its basal attachment.

Though the anterior half of postterminal centrum 1 apparently always fuses into the terminal vertebra in the Clupeoideae, the fate of the more posterior centrum elements seems to vary. Thus, in *Clupea*, judging from Ramanujam's figures (1929, figs. 26, 27), the posterior half of postterminal centrum 1 fuses with the base of hypural 3; the same thing has probably occurred in *Chirocentrus* (Text-fig. 6)

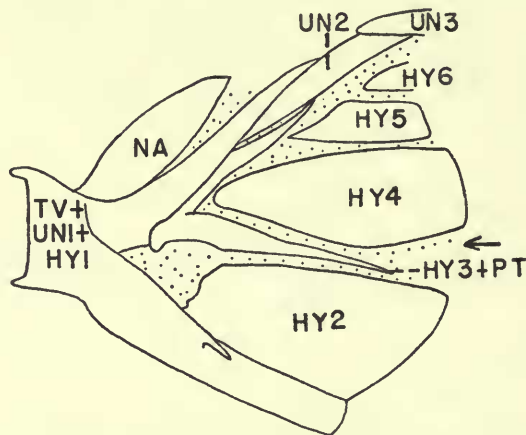


FIG. 7. Terminal vertebra and associated structures of *Dussumieria acuta*,  $\times 7\frac{1}{3}$ .

and the majority of Clupeoideae. In *Chirocentrus*, therefore, the element labelled PT is probably postterminal centrum 2, fused with such centrum elements as may occur behind it. From Hollister's figures (1936, figs. 40-45) it would appear that in the dussumieriid *Jenkinsiella* and perhaps in the engraulid *Anchoviella*, by contrast, the whole of postterminal centrum 1 fuses with the terminal vertebra. Finally, in *Dussumieria* it seems that the posterior half of postterminal centrum 1 has fused not only with the centrum elements behind it but with the base of hypural 3 as well. *Dussumieria* also differs from the other Clupeoideae examined in the fusion of hypural 1 with the terminal vertebra and the anterior uroneural.

*Superfamilies Chanoidae, Phractolaemoidae, and Knerioidae.* The caudal fin of *Chanos* differs in no very essential way from that of the herring-like fishes. The uroneural is completely fused at its base with the terminal vertebra, but the first hypural is merely suturally articulated. In the single large specimen examined neither hypural 2 nor 3 has any connection with a centrum. The one significant difference from the herrings would appear to be that the median projection between the basal wings of the uroneurals is low, and just above it, extending along the

upper surface of the uroneural is a single long rod, presumably an epural. This structure is quite reminiscent of that in *Alepocephalus* (see Text-fig. 1) though little else about the caudal skeleton is similar.

The caudal skeletons of *Phractolaemus* and *Kneria* are in turn very similar to *Chanos*, differing from that of the herrings in approximately the same way as *Chanos* does. However, there are only 13 branched rays in the rounded caudal of *Phractolaemus*.

*Superfamily Gonorhynchoidea*. The caudal skeleton of *Gonorhynchus* (Text-fig. 8), as might be expected from the general consolidation of skeletal parts, shows a very

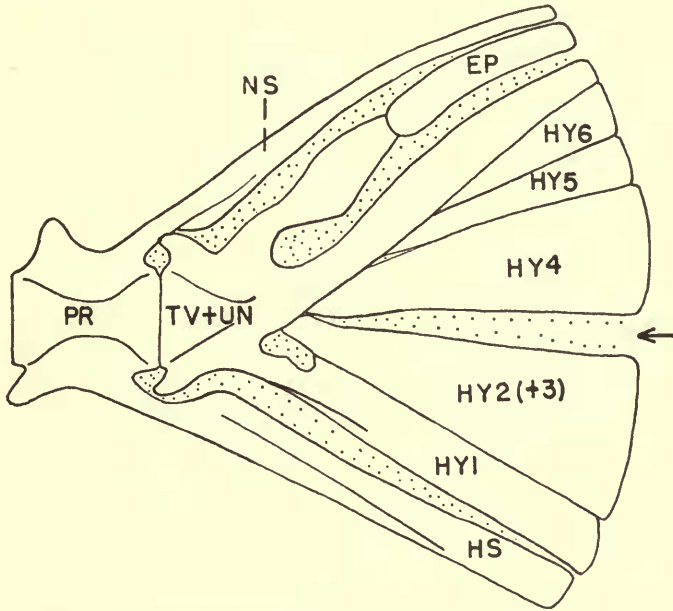


FIG. 8. Caudal skeleton of *Gonorhynchus greyi*,  $\times 7\frac{1}{2}$ .

high degree of fusion for the isospondylous fishes. Not only are the uroneurals ankylosed to one another and to the terminal vertebra along with hypural 1, but hypurals 2 and 3 appear to have fused with one another. In general appearance the caudal skeleton of *Gonorhynchus* bears considerable resemblance to that of *Dussumieria*, but whether this is a result of convergent evolution or of genetic relationship remains in doubt. In any event, the caudal skeleton of *Gonorhynchus* gives no indication of relationship with the Osteoglossoidae, and its 17 branched rays would militate against a possible derivation from *Hiodon*.

*Suborder Stomiatoidei*. Among the stomiatoid fishes the caudal skeletons of *Photichthys* (Text-fig. 9) and *Gonostoma* were the only ones available. These two differ considerably from one another. In *Photichthys* neither the anterior uroneural nor hypural 1 is fused with the terminal vertebra, but in *Gonostoma* both appear to be. In both genera there are the usual 17 branched caudal rays.

*Superfamily Salmonoidae.* The salmonids, thymallids, and coregonids (these terms are used here for groups of genera) all have a very characteristic and primitive caudal skeleton (Text-fig. 2). The anterior uroneural on either side bears a high crest between which the front ends of the epurals project. Two postterminal centra are visible; hypurals 2 and 3 articulate with the first of these, but the base of hypural 2 also extends somewhat forward on to the terminal vertebra. *Salmo* and *Salvelinus* have a well-developed neural spine on the first preterminal vertebra (Text-fig. 2), but in two skeletons of *Thymallus* (see also Lotz, 1864, pl. 10) and one of *Coregonus*

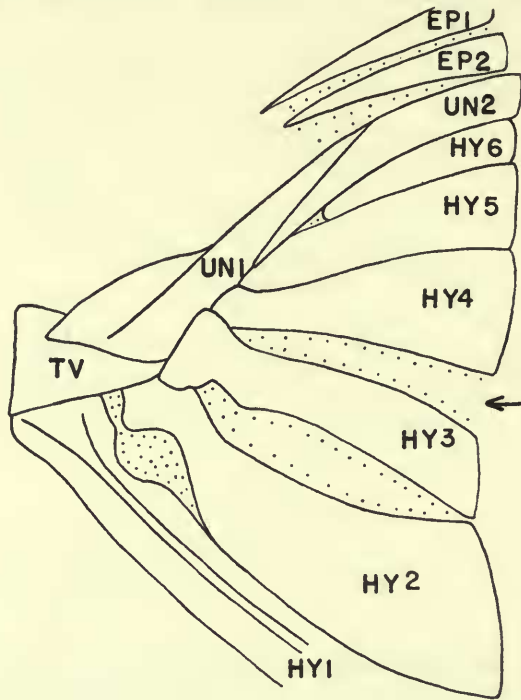


FIG. 9. Terminal vertebra and associated structures of *Photichthys argenteus*,  $\times 7\frac{1}{3}$ .

the epurals extend forward over but do not connect with the neural arch of the preterminal vertebra, thus replacing the neural spine in *Salmo*.

*Superfamily Argentinoidae.* Among the Argentinoidae the only skeleton available is one of *Argentina*. This is here illustrated (Text-fig. 10) despite the strong possibility that the articulation between hypural 1 and the terminal vertebra is abnormal. Other available figures of the Argentinoidae are those of *Opisthoproctus* (Trewavas, 1933, pl. 2) and of *Macropinna* and *Nansenia* (Chapman, 1942b, fig. 6 and 1948, fig. 12 respectively). All of these show the typical salmonoid neural and hemal spine expansions. They may, however, be separated from members of the Salmonoidae by the fact that the anterior uroneural never extends forward of the terminal vertebra and from the Osmeroidae by the presence of at least one postterminal centrum.

Subsequent examination of two stained specimens, 38 and 46 mm. in standard length, of the bathylagid *Leuroglossus stilbius* (kindly loaned by D. M. Cohen), shows the same basic structure described above. However, the salmonoid flanges are entirely lacking on the smaller and only slightly developed on the larger example. As compared with *Argentina*, there are, in *Leuroglossus*, only two uroneurals, which are very slender, and the anterior of these is fused with the terminal vertebra. The postterminal centrum is considerably smaller than that of *Argentina* (Text-fig. 10), and only hypural 5 articulates with it. Also, *Leuroglossus* has no epurals.

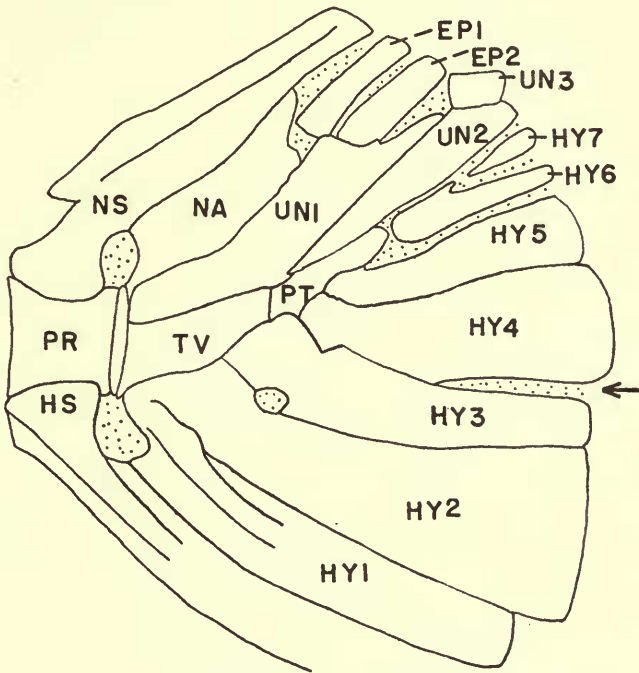


FIG. 10. Caudal skeleton of *Argentina silus*,  $\times 6\frac{2}{3}$ .

*Superfamily Osmeroidae.* Of the members of the Osmeroidae mentioned below, all but the Salangidae and *Lovettia* have the typical salmonoid neural and hemal spines (Text-fig. 5). None of them show a postterminal centrum or for that matter any other caudal resemblance to the esocoids. Though there is considerable variation among the members the most striking skeletal difference is that in *Retropinna* and *Galaxias* (Text-fig. 11) the anterior uroneural is not fused with the terminal vertebra whereas in *Hypomesus* (Text-fig. 5), *Plecoglossus* (Text-fig. 12), *Aplochiton*, and the salangid *Leucosoma* it is. The caudal skeleton of the last-named genus is quite different from all of the others.

In one respect the caudal fins of the southern Osmeroidae differ from those of the northern members of the group (also from the Argentinoidae and Salmonoidae). All of the latter, including the salangids and *Plecoglossus*, have 17 branched caudal

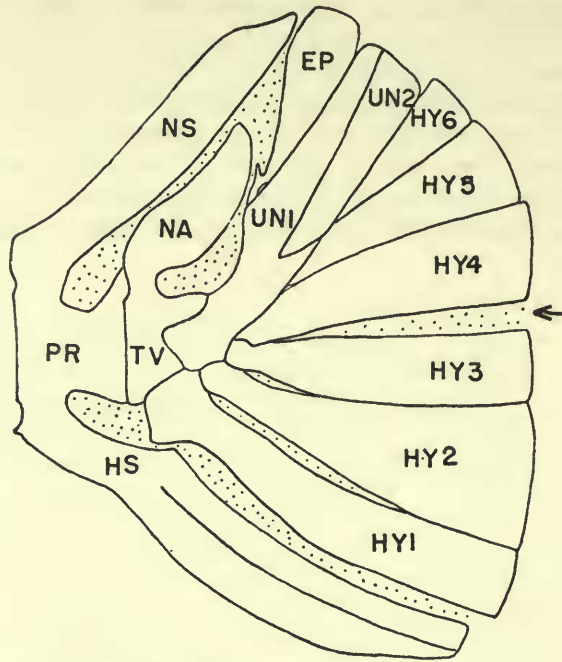


FIG. 11. Caudal skeleton of *Galaxias fasciatus*,  $\times 6\frac{2}{3}$ .

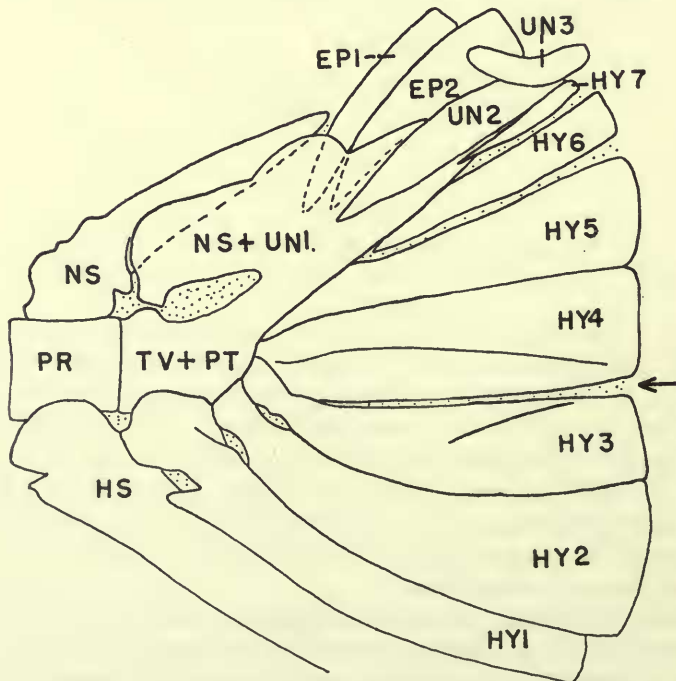


FIG. 12. Caudal skeleton of *Plecoglossus altivelis*,  $\times 8$ .



rays. In the southern *Retropinna* and *Prototroctes* there are 16 branched caudal rays; and in *Aplochiton*, *Lovettia*, and *Galaxias* 14.

*Suborder Esocoidei.* The caudal skeletons of *Esox* (Text-fig. 3) and of *Umbra* are quite similar. That of *Umbra* appears the more primitive of the two, with six "hypurals" of about equal size between a narrower strut above and below. The upper of these struts is the uppermost hypural; the lowermost is the hemal arch from the second preterminal vertebra, the first preterminal vertebra giving rise to one of the broad "hypurals". In seven specimens of *Esox lucius* for which caudal rays were counted, five had 17 branched rays and two 16; for three specimens of *Umbra krameri*, two had 9 branched rays and one 8.

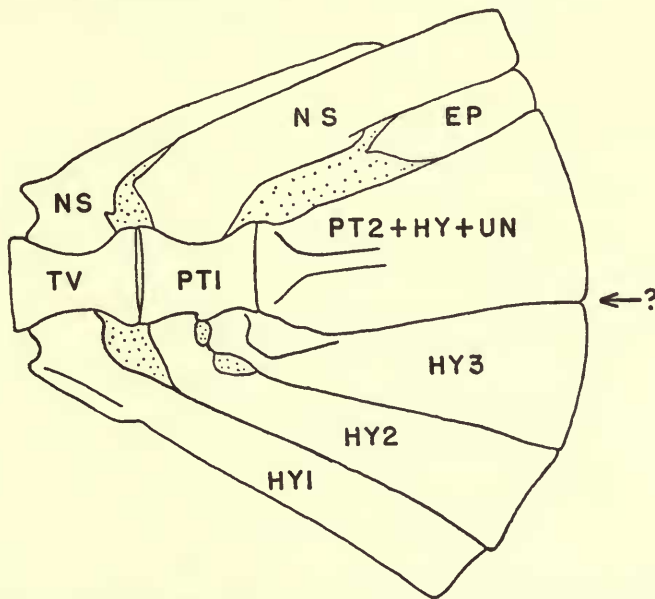


FIG. 13. Caudal skeleton of *Osteoglossum bicirrhosum*,  $\times 5\frac{1}{3}$ .

*Superfamily Hiodontoidae.* As previously mentioned, one of the most primitive of isospondyloous caudal skeletons is certainly that of *Hiodon*. In two skeletons examined, one of *H. tergisus* and one of *H. alosoides*, considerable variation appeared, not only from fish to fish, but on the two sides of the same fish. Thus the skeleton of *H. alosoides* has three uroneurals on one side (Text-fig. 4) and four on the other. In *H. tergisus* both the terminal and the first postterminal centra have double neural arches, and the anterior tip of the single epural runs in between but is free from the sides of the posteriormost arch. In *H. alosoides* (Text-fig. 4) both the terminal and the first postterminal vertebrae have single neural arches with spines that nearly reach the caudal fin base. Nine specimens of *H. alosoides* and one of *H. tergisus* examined all had 16 branched caudal rays.

*Superfamilies Osteoglossoidae and Notopteroidae.* The caudal skeletons of *Osteoglossum* (Text-fig. 13), *Pantodon*, and *Heterotis* (Text-fig. 14), while showing strong

similarities to one another, are so different from those of all the foregoing isospondyloous fishes as to be somewhat difficult to interpret. (*Notopterus*, see Whitehouse, 1910b, pl. 47, fig. 6 is even more specialized in the same direction, and a skeleton of *Arapaima* was not available.) Presumably, the terminal vertebra is that preceding

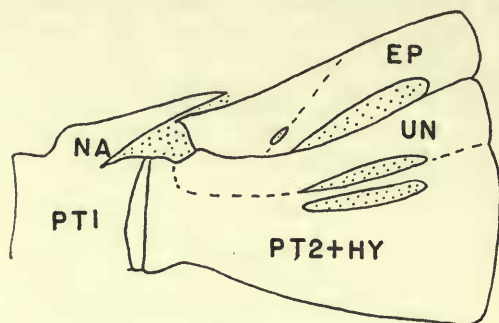


FIG. 14. Part of caudal skeleton of *Heterotis niloticus*,  $\times 4\frac{2}{3}$ .

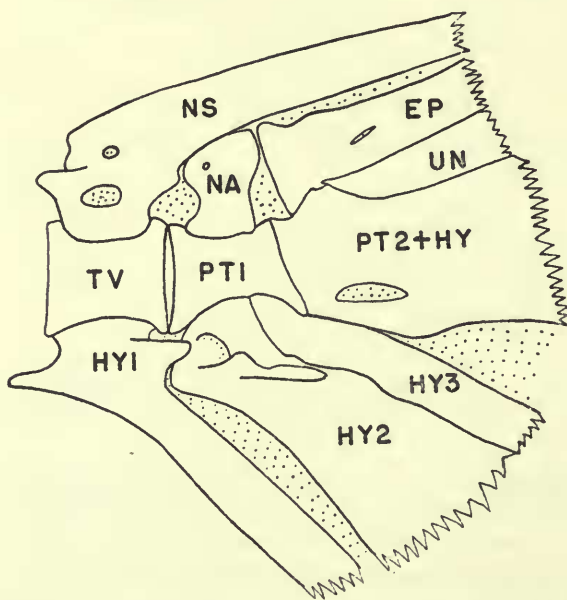


FIG. 15. Caudal skeleton of *Mormyrus caballus*,  $\times 5\frac{1}{2}$ .

the one to which two hypurals are attached. If this is correct, postterminal centrum 1 is present in an unusually complete form, and postterminal centrum 2 has fused with the large upper hypural plate and with the uroneurals as well (the latter fusion is incomplete in *Heterotis*, Text-fig. 14). Though any other interpretation of these caudal skeletons raises even more difficulties, the one just given presents three: first, hypural 3 in *Osteoglossum* has lateral flanges that are not found elsewhere in

isospondylous fishes; second, postterminal centrum 1 in *Osteoglossum* has a neural spine instead of the usual epural structure; finally, and most oddly, the uroneurals in all three genera under consideration fuse with postterminal centrum 2 instead of with the terminal vertebra. Because of this last peculiarity, the alternate interpretation that what is here called postterminal centrum 2 is really the terminal vertebra deserves serious consideration. In any event, it is difficult to see how the caudal structure of these fishes has been derived from any of the isospondylous groups, including *Hiodon*, dealt with up to here. *Heterotis* has only 12 branched caudal rays, and *Osteoglossum* 14.

*Order Mormyriiformes.* The caudal skeleton of *Mormyrus caballus* (Text-fig. 15) is basically very similar to those of *Heterotis* and *Osteoglossum*. The main differences lie in the flange on hypural 2 and the number of caudal rays in *Mormyrus* (16 branched).

#### DISCUSSION

Two subjects call for discussion. One is the functional significance of the different types of caudal skeletons noted above. The other concerns the bearing of the caudal structure on the limits of the order Clupeiformes.

Two aspects of the relation between structure and function will be considered<sup>1</sup>. The first of these concerns the elongate uroneurals of the primitive isospondylous fishes. According to Regan (1910a) and Ramanujam (1929) the uroneurals are, at least primarily, modified portions of neural arches of postterminal centra. Whatever their derivation, the elongation of these uroneurals in the so-called primitive isospondylous caudal skeleton is in itself a specialization. The only obvious explanation for these long uroneurals is that they stiffen the upturned terminal portion of the vertebral column. With the more abrupt upturning in this area found in advanced members of both the clupeoid and salmonoid lineages, the uroneurals, which start out as one or more shields along the sides of the postterminal centra, develop into struts which are at first wedged into the terminal vertebra and in more "advanced" forms fuse with it. Apparently a short, anchored strut serves here better than a long cover.

The second functional aspect has to do with the relationship between the caudal skeleton and the shape of the tail. In a very broad sense there is a correlation between these two features. Very generally, when the tail is forked the caudal skeleton is divided into distinct upper and lower portions, but when the tail is rounded the posterior outline of the hypurals is rounded, often with a number of hypurals of subequal size (e.g., *Amia*, *Umbra*) or with a central one somewhat larger than the others as in the cods. However, this relationship is far from strict. For example, the round-tailed serranid *Epinephelus* has the caudal skeleton of a typical fork-

<sup>1</sup> In this discussion the caudal skeleton is treated as if it were an independent functional unit. Obviously it is not, for beside providing an axis for the basal articulation of the caudal rays it serves as a source of attachment for some of the caudal musculature (cf. Hinderesson, 1910; Schmalhausen, especially 1913; and Greene and Greene, 1914) and for the transmission of the blood vessels and nerves to the caudal fin. However the role that these various functions have played in the evolution of the caudal skeleton are almost entirely unknown at the present time and have consequently been left out of consideration.

tailed fish. Conversely, the fork-tailed *Mormyrus* has a caudal skeleton that should belong to a round-tailed fish. Apparently the shape of the tail takes a very long time to imprint itself on the structure of the caudal skeleton.

Similarly there seems to be a relationship, though again not a strict one, between the shape of the caudal fin and the number of caudal rays. In fork-tailed fishes the number is usually constant within groups. Indeed the basic number of 17 branched caudal rays runs through two of the four isospondylous lineages postulated here. However, a rounded caudal is often associated with a lower (and variable) number of principal caudal rays. Presumably, in a fork-tailed fish the greatest strength and functional importance lies in the outermost principal caudal rays which form rigid limits to the fin. In round-tailed fishes these outer rays lose their significance and the fin tapers from the middle to above and below. One is inclined to wonder whether those fork-tailed isospondylous fishes with some lower caudal count than the typical one, e.g., *Hiodon*, *Aplochiton*, have not had some round-tailed ancestors?

With regard to the information caudal structure can provide on the limits of the order Clupeiformes, there are only three groups that need be considered here: the haplomous, mormyroid, and iniomous fishes. Each of these has been included in or excluded from the Clupeiformes, depending on the classification adopted.

The first two of these groups have already been dealt with. Suffice it to say here that so far as the caudal skeleton is concerned the haplomous fishes appear to be as primitive as any of the isospondylous fishes. Since they stand at the base it is impossible to derive them from any other modern isospondylous fish, so far as the caudal skeleton is concerned.

The mormyroid caudal skeleton seems clearly to have been developed from the type now found in *Heterotis*. The structural inference, as already noted, is that the mormyrids retain not only the imprint established in a round-tailed form, but one of a peculiar and definitely identifiable type.

Among the iniomous fishes (Scopeliformes) only skeletons of *Neoscopelus*, *Lampanyctus*, *Aulopus*, and synodontid fishes have been available for examination. The caudal structure of these seems to be somewhat more primitive than that of many isospondylous fishes in that one postterminal centrum is clearly visible. In certain features, e.g., the flanged uroneural, these iniomous caudal skeletons appear to approach the salmonoid Clupeiformes; however, they lack the expanded posterior neural and haemal spines of the salmonoids. In sum, there is little beyond an indication of possible relationships here.

Whether any or all of the three groups discussed above should be included in or excluded from the order Clupeiformes will, of course, depend in the first place on the nature of the whole animals, not just their tails, and in the second on a consensus of human opinion regarding what constitutes a fish order.

## SECTION 2. THE CLASSIFICATION AND RELATIONSHIPS OF THE SALMONOID FISHES

The members of the Suborder Salmonoidei (as defined here) today are the dominant fishes in the coldest fresh water of both hemispheres. They are also represented in

the temperate and arctic regions of northern seas by one group (Osmeridae) and in deeper oceanic waters by another (Argentinoidae<sup>1</sup>).

It is hardly surprising that there should be difficulty in defining as large and varied an assemblage as the salmonoids. Regan (1929) and others have differentiated them from the clupeoid groups by the absence or incompleteness of the oviducts. However, Kendall (1921) demonstrated that the oviducts of *Salmo* and *Osmerus* "are not radically different from those of other isospondylous fishes". Regan (1913a: 289) gives the following additional salmonoid characters: an adipose fin usually present, one supramaxillary or none, and parietals well developed. Probably the most useful of these three features for purposes of differentiation is the adipose fin, for it is found elsewhere in the isospondylous fishes only among the stomiatoids and the Rosauridae. However, there are salmonoids (*Galaxias*) and salmonoid derivatives (the haplomous fishes) in which the dorsal fin has moved far back on the body and presumably squeezed out the adipose fin (Garstang, 1931: 246-250). An adipose is also lacking in at least one of the oceanic salmonoids (*Microstoma*). An additional diagnostic trait of most salmonoids is that the last few "preterminal" vertebrae have laterally compressed neural and hemal arches, forming a flange above and below the posterior portion of the vertebral column (see previous section). This flange seems to be lacking only in the neotenic *Lovettia* and the Salangidae among the salmonoid skeletons examined. At least the posteriormost of these neural and hemal spines lead out to a series (usually about 10) of characteristic small, curved, accessory rays; these occur prominently in both *Lovettia* and the salangids. A final trait that will apparently distinguish the salmonoids (and haplomous fishes) from the herrings and their relatives is the absence of a lower series of intermuscular bones, i.e., the series that articulates proximally with the base of the lower ribs (cf., Emelianov, 1935.)

The present classification of the salmonoid families stems from Regan (1913a: 289). There, he differentiates the families as follows:

- " I. An orbitosphenoid; an opisthotic; a mesocoracoid; vertebrae upturned at base of caudal fin . . . . . I. SALMONIDAE
- II. An orbitosphenoid; no opisthotic; no upturned vertebrae; mesopterygoids toothless.
  - A mesocoracoid; parapophyses inferior . . . . . 2. ARGENTINIDAE
  - No mesocoracoid; parapophyses lateral . . . . . 3. MICROSTOMIDAE
- III. No orbitosphenoid; no opisthotic; no upturned vertebrae; mesopterygoid toothed (absent in the Salangidae).
  - A. A mesocoracoid; maxillaries dentigerous, entering gape . . . . . 4. OSMERIDAE
  - B. No mesocoracoid; maxillaries dentigerous, entering gape.
    - Head compressed; mesopterygoid well-developed dentigerous; ribs ossified . . . . . 5. RETROPINNATIDAE
    - Head strongly depressed; no mesopterygoid; ribs not ossified . . . . . 6. SALANGIDAE
  - C. No mesocoracoid; maxillaries toothless, behind praemaxillaries.
    - Praemaxillaries not extending whole length of maxillaries; roof of myodome unossified; no adipose fin. . . . . 7. GALAXIIDAE
    - Praemaxillaries nearly reaching extremities of maxillaries; roof of myodome ossified; an adipose fin . . . . . 8. HAPLOCHITONIDAE"

<sup>1</sup> The name Argentinoidae, rather than Opisthoproctoidae, will be used throughout this paper for the perhaps over-simple reason that the most recent workers on the group (Hubbs, 1955; Bertelsen, 1958; and Cohen, 1958) seem to prefer the former name.

With regard to this classification, Regan goes on to say (op. cit.: 290) :

“ It is of some interest to note that the Galaxiidae and Haplochitonidae are related to, but more specialized than, the Osmeridae, or Smelt family, of northern seas. *Retropinna*, from the coasts and rivers of Australia and New Zealand, is still nearer to the Galaxiidae and Haplochitonidae.”

Subsequent work by Trewavas (1933), Parr (1937), and Chapman (1942a, 1942b, 1943, and 1948) has abundantly shown that the members of Regan's section II—including his Argentinidae and Microstomidae—are rather widely divergent from the other salmonoid fishes. Characteristic features of the group are the toothless upper jaw, the pelagic eggs, etc. The classification of the families within the group seems to be rather controversial (cf., the above papers, Hubbs, 1953, and Bertelsen, 1958) but the subject will not be entered upon here.

Similarly the members of Regan's (1913a) section I may be readily distinguished from all other members of the suborder by the three upturned caudal vertebrae. (Other members of the suborder have one or, at most, two.) Whether the family Salmonidae should be interpreted in the broad sense of Regan (1913a) or whether the Thymallidae and/or Coregonidae should be split off as separate families are matters that can best be left to those more familiar with these fishes to decide. However, the assignment of the fossil Thaumaturidae by Voigt (1934), Berg (1940) and others to the salmonid group seems to be open to some question. The typical salmonoid flanges formed by the last few neural and hemal spines are lacking, as is the adipose fin (acc. Voigt) ; the upward inflexion of the last three vertebrae shown in Voigt's pl. 2, fig. 5 is not salmon-like and is, in any event, not duplicated in the specimens shown in pl. 1, figs. 1 and 2 ; and the posterior position of the dorsal is more reminiscent of the haplous fishes than of the salmonids.

The last group of salmonoid fishes—section III of Regan—contains a rather diverse assemblage of fishes. It can, however, be immediately divided into a northern group of families—Osmeridae, Plecoglossidae, and Salangidae—with 17 branched caudal rays, and a southern hemisphere group—Retropinnidae, Aplochitonidae, and Galaxiidae—with fewer branched caudal rays. This subdivision is in line with Regan's (1913a) statements quoted earlier. Nevertheless both groups are quite varied within themselves, and each has given rise to a series of specializations partly paralleled within the other. Thus the northern *Plecoglossus* with its specialized dentition to some extent resembles the southern *Prototroctes* with its small flexible teeth, and the northern neotenic salangids are partly duplicated in the southern neotenic *Lovettia*.

The salmonoid allocation of the three southern hemisphere families remained uncontested until Chapman (1944), on the basis of an osteological study of *Aplochiton*, transferred the Aplochitonidae, Galaxiidae, “ and very probably the Retropinnidae ” to the haplous fishes. Subsequent authors, e.g., Schultz and Stern (1948) and Wilimovsky (1951), have generally accepted Chapman's allocation. However, Blackburn (1950), from an investigation of the biology of the aplochitonid *Lovettia seali*, points out “ that the life history of this species is similar to that of various salmonids, which makes the author incline to the views of Regan and Jordan ” with regard to its systematic position.

In view of this difference of opinion, the British Museum material of the southern hemisphere forms has been examined. A general review of these, at least insofar as their systematic position is concerned, is undertaken in the following paragraphs.

In general the three southern families can be divided into two groups—the anadromous retropinnids and aplochitonids (*Prototroctes*?) with an adipose fin and a forked caudal, and the fresh-water or catadromous galaxiids without an adipose fin and with a rounded caudal.

The galaxiids would appear to be a fairly homogeneous group even though they are represented in southern South America, southern Africa, New Zealand, Tasmania, Australia, and presumably New Caledonia. Regan (1905) has an early revision of the family; more recently Scott (1936, etc.) and Stokell (1945, etc.) have worked on the systematics of the group. Swinnerton (1903) has written on the osteology of one of the species.

By contrast with the galaxiids, the retropinnids and aplochitonids are most diverse. The Retropinnidae has only a single Australian and New Zealand genus revised by Stokell (1941). The Aplochitonidae contains three very different genera: a fairly normal *Aplochiton* from southern South America and the Falkland Islands, *Proctotroctes* with a highly specialized dentition and with two almost if not entirely extinct species from Australia, Tasmania, and New Zealand, and the neotenic *Lovettia* from Tasmania. As already noted, Chapman (1944) has a paper on the osteology of *Aplochiton*, and Blackburn (1950) has published on the biology of *Lovettia*. A general account of the New Zealand forms of all three families is to be found in Stokell (1955).

In external characters, aside from those already mentioned, *Retropinna* and *Proctotroctes* are scaled; the other southern genera are naked. *Retropinna* has somewhat the look of, and is called, smelt (Stokell, 1955: 9-18, pls. 4 and 5) whereas *Proctotroctes* looks rather like a *Coregonus* (Stokell, 1955: 41-44, pl. 13). *Aplochiton* is more trout-like (Eigenmann, 1927: pl. 15); *Lovettia* has a definitely larval appearance (Blackburn, 1950, pls. 1 and 2); and the galaxiids (Stokell, 1955: 19-40, pls. 6-12) have somewhat the look of the northern *Umbra*.

So far as I can see the rather variable fin counts have no significance for the classification of the group as a whole except for the caudal. Judging from counts in a single specimen of each genus, *Prototroctes* and *Retropinna* have 16 branched rays, whereas *Aplochiton*, *Lovettia* and *Galaxias* have 14 branched. All of these genera have the typical salmonoid accessory rays (see previous Section) at the front of the caudal above and below.

The dentition of these southern hemisphere forms is most varied. At the one extreme are certain species of *Retropinna* (Stokell, 1941) in which there is a long posterior portion of the maxillary, a short premaxillary, a crescent-shaped vomer, palatines, mesopterygoid, tongue, a long bone covering the basibranchials, pharyngeals, and dentary all with large teeth. At the other extreme is *Prototroctes* with fine, peculiarly-shaped, flexible teeth in the upper jaw and apparently none in the lower.

The maxillary is also variable. In the single genus *Retropinna* it may be toothed or toothless (Stokell, 1941: pl. 55). In the three genera of the family Aplochitonidae

the toothless maxillary is excluded from the gape as effectually as it is in the perch-like fishes. A supramaxillary seems to be consistently absent.

In *Galaxias* and *Lovettia* the premaxillaries appear to be slightly protractile; in both these genera they have rudimentary anterior pedicels.

With regard to the skull the parietals meet on the midline except in *Lovettia*. In a ripe female specimen of *Lovettia* both the frontals and parietals are elongate bones running along the superolateral borders of the skull. The whole median area of the skull roof is merely membranous, with the brain clearly visible.

The anterior ends of the frontals project well forward over the ethmoid, not only in *Lovettia* but in all the other southern genera as well. There are no proethmoids in any of them and what Chapman describes as proethmoids in *Aplochiton* (1944 : 150, fig. 1) are not separate elements in British Museum specimens but are merely anterior prongs of the frontals. (If these anterior portions somehow came to develop as separate elements in the northern haplomous fishes, would they not be proethmoids?)

Whether the mesethmoid is cartilaginous or bony in *Lovettia* is impossible to say; it is certainly an endochondral formation. However, in *Galaxias* (cf., Swinerton, 1903) there is a dermal mesethmoid as well.

I have not seen an orbitosphenoid in any of the southern hemisphere forms.

At the back of the skull the small supraoccipital is excluded from the foramen magnum in all the southern genera.

In the suspensorium the large mesopterygoid is usually toothed in southern forms. The metapterygoid extends forward over much but not all of the quadrate. There seems to be no knob behind the palatine for articulation with the lateral ethmoid (prefrontal). As to the ectopterygoid, it and the palatine seem to be fused into a single long, mostly toothed bone in *Retropinna*. However in *Prototroctes* the two elements are separate.

The suboperculum is a rather large bone forming part of the gill cover in all except *Lovettia*. In *Lovettia*, the suboperculum gives the distinct impression of being the seventh (and terminal) branchiostegal.

In the pectoral girdle, none of the southern forms has a mesocoracoid.

In the caudal skeleton there are never any visible "postterminal centra" (see previous section). The anterior uroneural may (*Galaxias*) or may not (*Prototroctes*) be fused with the "terminal vertebra". In all, except *Lovettia*, the salmonoid flattening of the last few neural and hemal arches is distinctly developed.

As to soft anatomy, oviducts appear to be lacking in the females. In adult males of *Lovettia*, which seems to be unique in this respect, the urinogenital openings move forward to just behind the pectorals. None of the southern genera have pyloric caeca. *Lovettia* has a closed air bladder quite unlike that of the osmerids, salmonids, or northern haplomous fishes including salangids (N. B. Marshall, personal communication).

With this background regarding the southern hemisphere Aplochitonidae, Retropinnidae, and Galaxiidae, it remains to compare them with the northern hemisphere Esocoidei and Osmeroidae.

The northern haplomous fishes have been defined by Chapman (1934 : 372) as



follows (and the definition has been accepted with little change by Berg, 1936, 1940, and 1955) :

“Physostomous teleosts with the pelvic fins abdominal ; cycloid scales ; paired proethmoids ; parietals separated by the supraoccipital ; maxillary forming part of the edge of the upper jaw but lacking teeth ; premaxillary not protractile ; head scaly ; the dorsal and anal fins far back on the body ; but without adipose fin, mesocoracoid, or orbitosphenoid, and with no true spines in the fins.”

As has already been noted, the southern hemisphere *Lovettia* has a closed air bladder ; none of the southern forms have paired proethmoids ; only *Lovettia* has the parietals in any degree separated by the supraoccipital ; the maxillary is excluded from the gape in the Aplochitonidae, and in some species of the Retropinnidae the maxillary is toothed ; in *Lovettia* and *Galaxias* the premaxillary appears to be slightly protractile ; none of the southern forms have scales on the head ; the dorsal in *Proctotroctes* is not especially far back ; and only the galaxiids lack an adipose.

If, then, the southern hemisphere families are included in the Esocoidei, only the following portions of Chapman's (1934) definition are left intact :

“Teleosts with the pelvic fins abdominal ; cycloid scales ; anal fin far back on the body ; without mesocoracoid or orbitosphenoid, and with no true spines in the fins.”

The above words would apply, except for the absence of a mesocoracoid, to most Osmeroidae, and in toto to the included family Salangidae.

This is not to say that the southern families do not have haplomous resemblances, for they do. Indeed, some, but by no means all, of the similarities between *Aplochiton* and the haplomous fishes which Chapman lists (1944 : 164) will hold for all three southern families. Two more may be added here. First the southern families, like the northern Esocoidei, lack pyloric caeca, whereas the northern osmeroids (except the Salangidae) have several to very numerous caeca. Second, the southern forms all have fewer than 17 branched caudal rays, whereas the northern osmeroids all have 17 branched rays ; in the northern haplomous fishes there is a reduction in caudal ray number except in *Esox*, and even here two of the seven specimens examined had fewer than 17 branched rays.

In comparing the southern families with the northern Osmeroidae, Chapman (1944 : 163) has already noted a number of differences, and several more may be added. The most important would seem to be the following : in the north a supra-maxillary, mesocoracoid, epipleural ribs, and pyloric caeca are present (except in the Salangidae), whereas in the southern forms they are absent ; and in the northern forms there are 17 branched caudal rays whereas there are 16 or fewer in the southern families. Admittedly these differences in the southern group are all modifications away from the basic salmonid type and in a haplomous direction. The same may be said of the posterior dorsal and anal position and the loss of an adipose in the galaxiids, which, of all the southern forms, have progressed farthest along this route. However, this direction has also been followed to a considerable extent by the northern salangids.

If, however, it is admitted that all three southern families are related and if the

most primitive features of these families are added together, we have a fish that is basically osmerid. In *Prototroctes* the dorsal is median and the adipose is well developed. In some species of *Retropinna* the maxillary is toothed and indeed the whole dentition is osmerid, with the teeth of the tongue and basibranchials biting between those of the palatines and mesopterygoids. At the other end of the fish the salmonoid flanges on the neural and hemal spines are present (except in *Lovettia*)

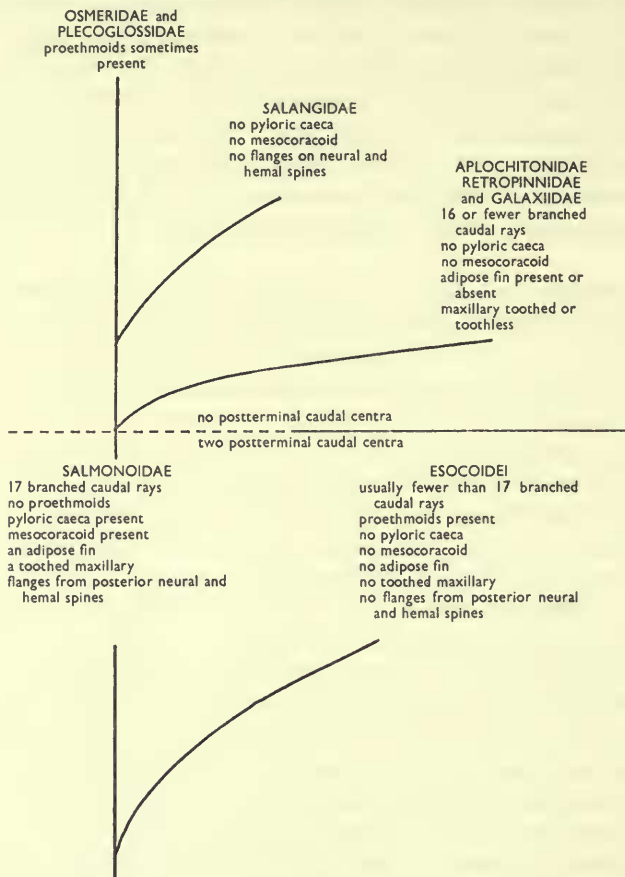


Diagram 2

along with the curved accessory caudal rays, and the caudal supporting skeleton is osmerid (see Section 1).

This last feature seems particularly important in view of the fact that the caudal skeleton of the haplous fishes is not only very different but far more primitive than that of the northern and southern Osmeridae. Finally, the anadromous life history of several of the southern forms recalls that of many salmonids. From all this it seems to the present author that the Aplochitonidae, Retropinnidae, and Galaxiidae are derivatives of a proto-osmerid stock that have evolved, some more and some less, in a haplous direction; and that this same direction has been followed a third time to a lesser extent by the Salangidae (see accompanying diagram).

That the Salangidae and the southern hemisphere Osmeroidae have departed in the same direction from the northern Osmeroidae is indicated by the characters listed in the diagram. But the similarities between the salangids and the aplochitonid *Lovettia* are even more striking. Both *Lovettia* and the salangids are more or less neotenic, anadromous fishes, with tremendous sexual differentiation. The sexual differentiation, however, is of a very different type in the two groups: in the salangid males, but not the females, there is a series of large scales above the anal fin, and the fin itself has a peculiar curvature in several of the median rays; in the adult male *Lovettia* the urinogenital papilla is just behind the pectoral fins. In the head of both, the posterior portion of the skull is very incompletely roofed by the frontals and parietals. Furthermore, these are the only two groups in the Salmonoidei that have no flanges on the preterminal neural and hemal spines.

In view of this it may appear that *Lovettia* and the salangids are closely related. Again I would prefer the hypothesis of parallel (neotenic) development. That *Lovettia* belongs with the southern osmeroids, and the salangids with the northern forms is indicated by the caudal ray count. In dentition, the salangids have a toothed maxillary typical of northern osmeroids, whereas *Lovettia* has a toothless maxillary excluded from the gape typical of the other two genera of aplochitonids. Additional characters for differentiating at least *Salangichthys microdon* from *Lovettia sealei* are the presence of a high (cartilaginous?) lump just behind the palatine for articulation with the lateral ethmoid (prefrontal) in *Salangichthys* and the absence of such a structure in *Lovettia*; the presence of a well-developed subopercle in *Salangichthys* whereas the subopercle resembles a free branchiostegal in *Lovettia*; the six branchiostegals of *Lovettia* vs. the four in *Salangichthys*; and finally the normal, open salmonoid air bladder in *Salangichthys* vs. the peculiar closed one in *Lovettia* (see above).

A final question regards the interrelationships of the members of the southern group. Berg (1940) separated the galaxiids as a distinct order, primarily on the basis of brain structure. Unfortunately, all that is known about the brain of these southern forms seems to be a single remark by Swinnerton (1903) regarding *Galaxias*. However, there are other features that set *Galaxias* apart from the other southern osmeroids. Among these may be mentioned the general body form and the catadromous habits.

Another line of differentiation within the southern section of the Osmeroidae is shown by *Lovettia* with its neoteny, sexual differentiation, and closed swimbladder. Such peculiarities would certainly warrant family differentiation from the aplochitonids, except that the Aplochitonidae is already a family of only three genera. Furthermore, the two remaining genera—*Prototroctes* and *Aplochiton*—are also very different from one another, and it seems preferable not to erect three separate families each with a single genus.

Nevertheless, the fact remains that the southern Osmeroidae are now represented by several highly differentiated forms. Indeed, the differentiation is as great as in the northern Osmeroidae.

So far as the haplous fishes are concerned, Berg stated in 1936 that the "Eso-coidei are a specialized group of Clupeiformes originating from Osmeroid fishes at the end of the Cretaceous". The present paper would tend, like that on *Aplochiton* by Chapman (1944), to demonstrate an even closer set of morphological links between

osmeroids and esocoids than was known to Berg. However, the primitive caudal skeleton of the haplous fishes indicates (see previous section) that *Esox*, *Umbra*, etc. have been derived from a somewhat less advanced salmonoid stock than the northern and southern Osmeroidae.

From the foregoing account, a classification (to superfamily) of the modern salmonoid fishes and their haplous derivatives may be written as follows :

Suborder Salmonoidei

Superfamily Salmonoidae

Superfamily Argentinoidae (= Opisthoproctoideae)

Superfamily Osmeroidae

Suborder Esocoidei

Superfamily Dallioideae

Superfamily Umbroideae

Superfamily Esocoidae

In this classification the three haplous superfamilies of Chapman (1934) and Berg (1940, 1955) have been accepted without any attempt at critical evaluation. As to the salmonoid superfamilies listed here, everyone admits that they are related ; the only question is how to express the relationships. Here, the salmonid and osmerid groups have been recognized as separate superfamilies, and the argentinoids have been demoted to a superfamily equivalent to them. The first action is taken because it seems advisable, where feasible, to segregate a basal stock that has given rise to a number of lineages from the advanced members of those lineages.

The place that the Argentinoidae should hold in relation to the other two salmonoid superfamilies is somewhat less clear. Nevertheless it can only obscure the relationship that undoubtedly does occur to set the Argentinoidae up as a suborder (Opisthoproctoidei of Berg, 1940, Chapman, 1942*a*, etc.) with a taxonomic rank equivalent to that of the salmonoids themselves. In the specializations of the head skeleton (Chapman, 1942*a* and *b*), in the loss of a ventral mesentery (Kendall, 1935, Table I), and in the caudal skeleton (see previous section), the Argentinoidae is more specialized than the Salmonoidae<sup>1</sup>. It would seem that the Argentinoidae is a much more divergent offshoot of the stock represented by *Salmo* today than is the Osmeroidae. But to express this greater divergence in a classification seems to lead to more incongruities than to consider them as a superfamily equivalent to the Salmonoidae and Osmeroidae.

### SECTION 3. THE GONORHYNCHOID FISHES AND THEIR RELATIONSHIPS

The single modern genus generally attributed to the suborder Gonorhynchoidei is *Gonorhynchus* (cf., Regan, 1929 ; Berg, 1940 ; Wilimovsky, 1951 ; etc.). The systematic position of the suborder has always been dubious. Ridewood (1905*b*), on the basis of a study of the skull of *Gonorhynchus greyi*, while emphasizing its isolated position, tentatively suggests a distant relationship with the salmonids.

<sup>1</sup> Another distinguishing character usually attributed to the argentinoids is the presence of a spiral valve in the intestine (cf., Kendall & Crawford, 1922). However, Cohen (1958 : 97, 98) has recently demonstrated that the "spiral valve" of argentinoids is not so diagnostic of that group as has usually been stated.

Regan (1929), in his synopsis of the isospondylous fishes, places the gonorhynchids at the end of the order, behind the mormyrids. His basis for this placement is that the gonorhynchids have the "parapophyses ankylosed with centra, appearing as strong processes". Subsequent authors, e.g., Berg (1940), Wilimovsky (1951), have generally accepted Regan's allocation.

That the parapophyses in *Gonorhynchus* are strong processes fused with the centra is true, but the value of this character in the classification of the isospondylous fishes seems dubious. For example, among the groups included by Regan in the section with *Gonorhynchus*, this genus and *Osteoglossum* have "strong processes" but *Hiodon* and *Mormyrus* appear to have none whatever, the ribs articulating directly with the centra.

A search for other characters that might indicate the relationships of *Gonorhynchus* discloses the following, all of which point toward an albulid-clupeid relationship. There are 17 branched caudal rays (this could equally well indicate a salmonoid ancestry). The caudal skeleton, except for the greater fusion of parts, resembles that of *Dussumieria*, the upright neural arch on the terminal vertebra being especially reminiscent of the clupeoids. Arising from the parapophyses are two sets of segmental bones; one of these undoubtedly represents the lower ribs, but the other seems to be the lower intermuscular bones. Lower intermuscular bones again are characteristic of the clupeoids and seem to be absent from most, if not all, other isospondylous groups.

As to relationships within the great clupeoid stock, it is here suggested that the gonorhynchids belong with the chanids, phractolaemids, kneriids, and cromeriids. These five groups are so widely different that any relationship between them is difficult to comprehend. Yet the following similarities may be marshalled.

In external characters, the gill membranes are always attached to the isthmus, and in the three African families the gill openings are considerably restricted. In all, the mouth is small and toothless, or nearly so. The preopercular border is free only below (*Chanos*), if at all.

In the head the maxillaries run forward behind the premaxillaries and nearly or quite meet on the midline. There are no supramaxillaries. A preorbital bone extends forward above the upper jaw nearly to the end of the snout (this is least developed in *Chanos*). The preopercle extends only a short way up the side of the head and there may be a suprapreopercular (*Phractolaemus* and *Chanos*) or a long tube-containing ossicle (*Kneria*) above it. The lower preopercular limb, however, runs well forward and forms the chief support for the quadrate. On the skull roof the frontals are large and the parietals are very small and almost restricted to the rear border of the skull, with the supraoccipital separating those of the two sides. The supratemporal commissure of the lateral line either runs across the parietals and supraoccipital through a series of superficial ossicles or through these bones themselves.

In *Gonorhynchus* and *Chanos* the exoccipitals send out a pair of prongs that roof the anterior portion of the spinal cord; in the flat-headed *Kneria* and *Phractolaemus* the projection of the supraoccipital serves the same purpose, with the walls of the first few neural arches forming the sides.

The lower intermuscular bones are present in *Chanos* and *Gonorhynchus*, apparently absent in *Phractolaemus* and *Kneria*. In *Gonorhynchus* the lower ribs are short and slight, and articulate with lateral expansions of the centra. In *Chanos* the ribs are large and their upper portions articulate directly with the centra, the lower by way of a bony nodule. In *Phractolaemus* and *Kneria* the ribs articulate directly with the centra but in the former the ribs are very strong, in the latter moderate. Admittedly, these vertebral characters show little relationship between the genera, but they are given because of their previous use in classification.

The caudal skeleton of all these groups (*Cromeria*?) is essentially the same.

As to mode of life, *Gonorhynchus* is today a purely marine fish, but the group to which it belongs is known from Eocene fresh-water deposits from America and Europe. *Chanos* is euryhaline, and the other three genera are restricted to fresh water. All five genera are tropical.

A good many of the similarities in these five groups may be primarily or secondarily related to the small size of the mouth in all these forms. It could therefore be that the small mouth has developed independently two or more times and that all of the other changes have followed as a matter of course. Some check on this possibility is offered by the members of the Argentinoidae, a small-mouthed group in the salmonoid stock. To some extent a parallel evolution is indicated between the Argentinoidae and the five groups taken up here, particularly with regard to jaw structure, suspensorium and the reduction in branchiostegal rays. However, there are a number of features in the five groups that are not duplicated in the Argentinoidae. Among these are the attachment of the gill covers to the isthmus, the loss of the normal upper portion of the preoperculum, the passage of the supratemporal commissure over or through the supraoccipital, the expansion of the anterior portion of the spinal canal, and the advanced form of the caudal skeleton.

To summarize, the argument presented here is not that *Gonorhynchus*, *Chanos*, *Cromeria*, *Kneria*, and *Phractolaemus* are closely related. Indeed, no two of them are. It merely seems to the author that each of the five is more closely related to the others than it is to anything else. If this is granted, then it becomes fairly easy to tie in the group, via *Chanos* and to some extent *Gonorhynchus*, with the general clupeoid stock<sup>1</sup>.

#### SECTION 4. A CLASSIFICATION OF THE MODERN ISOSPONDYLOUS FISHES

The systematics of the living isospondylous fishes have received a great deal of attention. Because of the excellent literature review by Wilimovsky (1951) only a sampling of papers on the subject need be mentioned here.

With regard to the general classification of the groups of Clupeiformes the deservedly classical papers are those of Ridewood (1904*a* and *b*, 1905*a*, *b*, and *c*). Unfortu-

<sup>1</sup> The British Museum (Natural History) material upon which the above account has been based consists of complete skeletons of *Gonorhynchus* and *Chanos*, somewhat incomplete skeletons of *Phractolaemus* and *Kneria*, and a stained and partially cleared skeleton of *Kneria*. Whole specimens of all genera mentioned have been examined. For the osteology of *Cromeria*, reliance has had to be placed on the paper by Swinnerton (1903). Ridewood's accounts of the head skeletons of *Phractolaemus* (1905*a*) and *Gonorhynchus* (1905*b*) have also been used.

nately Ridewood studied only the head skeletons of a limited number of isospondylous groups. Regan (1913*a*) dealt briefly with the classification of the salmonoid fishes and in 1929 presented a synopsis of the full order. Berg's (1940) volume introduced some rather drastic innovations. Chapman (1934-1948) has written a number of valuable papers on the relationships of individual members of the group, and Norman (1957) gave a key to the suborders, families, and genera.

Besides the above and many other papers dealing more or less directly with isospondylous classification, a large number of works bear indirectly on the subject. For example, Ford (1937) took up variations in the vertebral column. Whitehouse (1910*a* and *b*), Regan (1910*a* and *b*), Hollister (1936, 1940), and Schaeffer (1949: 13, 14) have taken up the caudal skeleton. Starks (1930) wrote the most complete account of the pectoral girdle. Frost (1925) took up isospondylous otoliths. Allis (1904), Wohlfahrt (1937), and Nybelin (1957) have dealt with the lateral line system of the head. Van Dobben (1935), Hofer (1945), Tchernavin (1953), Günther and

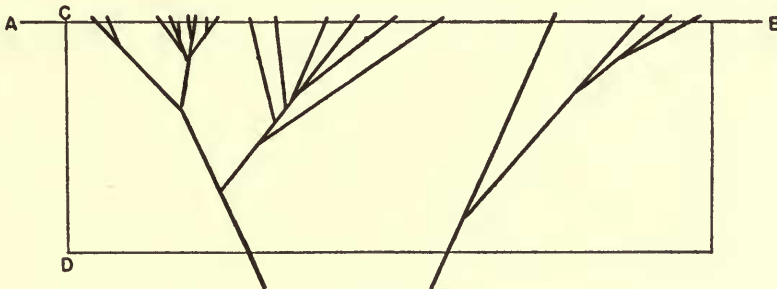


Diagram 3

Deckert (1953, etc.) and Kirkhoff (1958) have taken up various aspects of the functional morphology of the head. As to soft anatomy, Bridge (1900), de Beaufort (1909), Svetovidov (1950, etc.), Jones and Marshall (1952), and O'Connell (1955) investigated the air bladder. Boas (1880) and Senior (1907, etc.) reported on the heart. Jacobshagen (1912) and Suyehiro (1942) have made comparative studies of the digestive system. Finally, Hyrtl (1856), Lagler and Kraatz (1945), Kapoor (1954), and Takahashi (1957) have dealt with the epibranchial organ.

Despite all of the work that has been done, the classification of the isospondylous fishes (Order Clupeiformes) remains unsatisfactory. Indeed, Berg (1940:417) has written: "This order, from which a series of higher orders has arisen, represents an artificial assemblage, its separate members, as may be seen from the diagnosis, differing greatly from one another. In time the Clupeiformes will be, doubtlessly, divided in many orders". Berg's view, I think, stems at least in part from a tendency to look at isospondylous classification at a single time level, for example AB of Diagram 3, whereas if a time dimension, CD, were incorporated into the concept, the "artificial assemblage" aspect would seem to largely disappear. In any event there are four main questions that need to be answered with regard to isospondylous classification. (1) What are the interrelationships of the living members? (2) What are the relationships between living and fossil members? (3) What are the limits of the group? (4) How can it be defined?

Here, no effort will be made to deal with fossil forms. The classification of fossil Clupeiformes is a large and important subject in itself, and one to which the present author can make little contribution as he has no first hand familiarity with fossil material.

The classification of modern isospondylous fishes that follows thus attempts to reconstruct phylogenetic relationships from a knowledge of fishes at only one time level and is consequently prone to all the pitfalls inherent in such a procedure. Yet there are certain points to be made in justification of such a classification. One is that it provides a corpus for the paleontologists to work from, with, or even against. More important, however, is the fact that ichthyologists working with modern fishes are obligated to do as much as they can with the fishes around them. There is virtually no chance that neotenic fishes like *Cromeria* and *Lovettia* will ever turn up in the fossil record. Indeed one is inclined to wonder whether the fossil record would not give a very peculiar picture of isospondylous classification because of the overrepresentation of some groups and the underrepresentation of others. Thus the salmonids are usually stream dwellers and are unlikely candidates for fossilization; the same might be said of the oceanic stomiatooids. Again, some of the most peculiar of the isospondylous fishes are from African fresh waters, and pre-Pliocene fish remains from that continent are as yet few. On the other hand certain of the isospondylous fishes, notably the herring-like forms, seem frequently to die in areas where they fossilize in relative abundance. Thus if the major groups of the paleontologist, e.g., the chirocentrids, do not always correspond to the major groups of the modern ichthyologist, that may merely mean a difference in viewpoint rather than an error in interpretation. Eventually, of course, a single classification of isospondylous fishes based on both fossil and recent material will have to be developed, but the time to attempt this hardly seems to have arrived.

As to a hard and fast definition of the Clupeiformes, that, as might be expected of any group so diverse, is impossible except in negative terms. Apparently about the best that can be done is as follows:

Caudal fin homocercal. No true spines in the fins. Pelvic fins abdominal and with more than 5 rays (although in the Notopteridae the pelvics are absent or rudimentary and few-rayed, and the Notopteridae, *Pantodon* and *Macristium* have subthoracic pelvics). Maxillary usually included in the gape. Scales, if present, cycloid (except *Gomorhynchus* and certain species of argentinids and osmerids). Air bladder, if present, physostomous (except *Lovettia*, stomiatooids, and Argentinoidae). Orbitosphenoid and mesocoracoid generally present; branched caudal rays most frequently 17. No Weberian ossicles. Lateral line, if present, not running low on sides. Snout not tubular. No electric organs.

With regard to the limits of the Clupeiformes, both the "upper" and the "lower" borders of the order have been the subject of controversy. Thus Saint-Seine (1949) removed *Elops* from the isospondylous fishes and placed it in the Halecostomi, and Nybelin (1957) has stated that *Elops* is as much a holostean as *Amia* or *Lepistosteus*. Here, *Elops* will be retained in the Clupeiformes, with the full realization that it becomes extremely difficult to place a lower limit on the order when fossil material is taken into account.



At the "upper" limit there are six groups of fishes that have been at times included in and at other times excluded from the Clupeiformes by modern authors. That the Anotopteridae, included "incertae sedis" by Berg (1940: 435), belongs among the iniomous fishes has been adequately shown by Maul (1946) and Nybelin (1946). Berg (1940: 436) creates a separate order for the Galaxiidae, but this family may apparently be returned to its usual place in the Clupeiformes (see Section 2). The Bathyclupeidae has been juggled about by various authors, sometimes landing in the isospondylous fishes, but it belongs with the percoids where Regan (1913*b*) placed it (N. B. Marshall). The three remaining groups are more controversial. The gymnarchid-mormyrid stock can be traced back with considerable certainty into the osteoglossid-notopterid group of isospondylous fishes. Nevertheless the Mormyriiformes seems to show sufficient specializations—e.g., in the electric organ and the brain—to justify separation at the ordinal level. The controversy regarding the iniomous fishes has a somewhat different basis. Their origin in the Clupeiformes cannot be traced by more than guesswork. However, the one character usually used to differentiate the iniomous from the isospondylous fishes is the exclusion of the maxillary from the gape in the former, and Chapman (1944) and others have pointed out that various isospondylous families also have the maxillary excluded. Thus the differentiation between the two orders breaks down, and Schultz and Stern (1948) have consequently merged them. Nevertheless, it does not seem justifiable to unite two groups just because all the members of one cannot be separated from all the members of the other by a single character. In the instance of the Myctophiformes and the Clupeiformes it is not even a question of where to draw the line in a continuous lineage, for the isospondylous fishes with the maxillary excluded from the gape (except possibly *Albula*) undoubtedly did not give rise to the iniomous fishes. But if the argument for merging the two orders seems weak, that for keeping them separate as is done here has, in this author's opinion, never been very convincingly presented. (The closest approach seems to be that of Marshall, 1955: 305). Finally, that the haplomous fishes belong in the Clupeiformes has been convincingly argued by Berg (1936, 1940), and further evidence for this allocation has already been presented in Section 2 of this paper.

## Order Clupeiformes (Isospondyli)

### Division I Clupei

#### Suborder I Elopoidei

##### Superfamily I Elopoidae

##### Superfamily II Albuloidae

#### Suborder II Clupeoidei

##### Superfamily I Alepocephaloideae

##### Superfamily II Clupeoidae

#### Suborder III Gonorhynchoidei

##### Superfamily I Chanoidae

##### Superfamily II Gonorhynchoideae

##### Superfamily III Phractolaemoidae

##### Superfamily IV Knerioidae

##### Superfamily V Cromerioidae

- Suborder IV Stomiatoidei
  - Superfamily I Gonostomoidae
  - Superfamily II Stomiatoidae
  - Superfamily III Astronesthoidae
- Suborder V Salmonoidei
  - Superfamily I Salmonoidae
  - Superfamily II Argentinoidae (Opisthoproctoidae)
  - Superfamily III Osmeroidae
- Suborder VI Esocoidei (Haplomi)
  - Superfamily I Dallioideae
  - Superfamily II Umbroidae
  - Superfamily III Esocoidae
- Division II Osteoglossi
  - Suborder VII Osteoglossoidei
    - Superfamily I Hiodontoidae
    - Superfamily II Notopteroidae
    - Superfamily III Osteoglossoidae

Certain final points regarding the classification of the isospondylous fishes presented above may be noted. First, N. B. Marshall has called my attention to the omission of three families of dubious systematic position: the Bathylaconidae (Parr, 1948), the Rosauridae (Tucker, 1954) and the Macristiidae (Regan, 1911). These are all families of oceanic fishes based on one or a few specimens. Any attempt to place them in one position or another within the Clupeiformes at the present time would be gratuitous, and it seems better to leave them *incertae sedis*. As to the better-represented groups, the classification of the superfamilies of Stomiatoidei and Esocoidei stand as they appear in Berg (1940), and the superfamily Alepocephaloidae is left as usual in the Clupeoidei. The author has almost no first hand knowledge of any of these groups.

Second, as a matter of practice this author believes that orders and suborders should be monophyletic but rather broadly interpreted. In contrast with Berg (1940), he would be very chary about the erection of orders and suborders for a few aberrant forms; these he would in general relegate to superfamilies (if such a higher category is needed). The reasoning behind this is that superfamilies are usually used by specialists, to whom the names of small divergent groups are significant, but are rarely incorporated in general classifications, where such names would generally have little meaning.

Finally, there remains the question of whether the Clupeiformes is polyphyletic. The evidence of the caudal skeleton would appear to be against such a conclusion. The caudal structures of the basal forms *Elops*, *Salmo*, *Esox*, and *Hiodon* are not only strikingly similar (Section 1), they are also widely different from anything among the recent members of the Holostei. Some of the ways in which they resemble each other and differ from the caudal skeletons of lower fishes seem to be of a type that would hardly have been developed independently twice, e.g., the three and only three hypurals to the lower caudal lobe, the peculiarities in the basal articulations

of these three hypurals (No. 1 with the terminal vertebra, and Nos. 2 and 3 with the first postterminal centrum), the long uroneurals, etc. Indeed if there is any indication of polyphyletic origin in the caudal structure of the Clupeiformes it would be between the osteoglossid-notopterid stock on the one hand and *Hiodon* with all the rest of the isospondylous fishes on the other. But such a split separating *Hiodon* from the osteoglossid groups seems untenable on any other ground than the caudal skeleton.

When all features are taken into consideration only two stocks (Divisions) seem distinctly separable within the order. One of these (Division II) contains today a small number of relict forms that are all, in their peculiar fashion, mixtures of primitive and specialized characters. To exemplify the basic nature of the stock no one fish can be selected; rather it is necessary to give a composite description based on the primitive features found in most of the Hiodontoidae, Osteoglossoidae, and Notopteroidae. If this is done it may be said that in Division II the parasphenoid remains primitive from three points of view. First, it never reaches the rear of the basioccipital; second, it sometimes retains a pair of projections for articulation with the suspensorium; and finally, it generally bears teeth. The last two features play a role in the general dentition and palatal construction in the stock as a whole; in these Division II appears to have remained primitive, quite in contrast to the evolution that has occurred in Division I. Throughout Division II, except *Heterotis*, the primary portion of the bite is between the parasphenoid and the tongue (cf., Hofer, 1945). Such bony articulations as occur on the top of the mouth are between the parasphenoid and the mesopterygoid, not from the ethmoid-prefrontal area via the palatines to the maxillary pedicels. Indeed, in Division II the palatines end anteriorly in a simple point and the maxillaries merely appear to be toothed cheek bones that have come loose posteriorly; they have no pedicels. However, if supramaxillaries are a primitive character, Division II has lost them. Also, in the vertebral column Division II would seem to have advanced farther along the road toward the fusion of elements than Division I, and in the caudal skeleton (aside from *Hiodon*) Division II seems to have evolved in a totally different way from Division I.

By contrast Division I is represented today by some primitive forms, notably the elopoids, that in most respects might stand as the ancestors of the whole division. Actually, *Elops* and *Albula* in certain characteristics, especially dentition, seem to form better prototypes for the stock than the Jurassic *Leptolepis bronni* (Rayner, 1937), for in dentition *L. bronni* seems already to have developed much of the specialization of the modern Clupeidae. Returning to modern forms, the Elopoidae and Albuloideae are the only superfamilies in the Division that have retained a parasphenoid dentition. In the others it has been totally lost, and when teeth reappear along the center of the mouth roof as in *Esox* they are on a backward projection of the vomer. The parasphenoid-mesopterygoid articulation is also lost in all modern forms though it is present in *Leptolepis bronni* (Rayner, 1937). On the other hand, a complicated cranium-palatine-maxillary articulation is usually present, giving the whole upper jaw structure an aspect rather similar to that of the higher fishes.

An important question regarding Division I is whether it contains within itself two or more independent lineages that are of equal value with Division II. One

such possible independent group is the *Gonorhynchidae*. If, however, *Gonorhynchus* is related to *Chanos*, as is suggested in Section 3 of this paper, then its pertinence to Division I would seem fairly secure. A more moot group, in this author's opinion, is the whole salmonoid-haplomous stock. There are only two items known to the author that might serve as an indication of a salmonoid-clupeoid relationship. One is that *Albula*, which is usually assumed to be related to the clupeoids, seems to show some similarity in the caudal skeleton to that typical of the salmonoids. The other is that the stomiatooids appear to be intermediate in certain respects between the salmonoids and the clupeoids: on the one hand some of the stomiatooids have the two supramaxillaries of the clupeoid fishes and *Elops*; on the other, many stomiatooids have the typical salmonoid adipose fin. Especially because of this puzzling link provided by the stomiatooids, it seems best to include the salmonoids in the same division with the clupeoids for the moment.

#### SYNOPSIS OF MODERN CLUPEIFORM FISHES TO SUPERFAMILY

- 1a. Parasphenoid extending nearly to the posterior end of the basioccipital or beyond.  
Parasphenoid never with lateral processes for articulation with the mesopterygoid; anterior ribs usually articulating with small parapophyses that are wedged into pits in the centra; branched caudal rays often 17. Division Clupei.
- 2a. Teeth present on the parasphenoid; a leptocephalous larval form.
  - 3a. A gular plate . . . . . Suborder ELOPOIDEI
  - 3b. No gular plate . . . . . Superfamily ELOPOIDAE
  - 2b. No teeth on the parasphenoid; no leptocephalous larval form. Superfamily ALBULOIDAE
  - 4a. Lower intermuscular bones usually present; photophores, if present, not in two rows along lower sides; posterior neural and hemal spines without antero-posteriorly expanded blades; no proethmoids.
  - 5a. Supramaxillaries usually present; gill covers free from the isthmus; branchiostegal rays 7 or more . . . . . Suborder CLUPEOIDEI
  - 6a. Two postterminal centra; no temporal foramen; black, deep-water fishes  
Superfamily ALEPOCEPHALOIDEAE
  - 6b. One or no postterminal centra; a temporal foramen; silvery, surface-living fishes . . . . . Superfamily CLUPEOIDEAE
  - 5b. No supramaxillaries; gill covers attached to the isthmus; branchiostegal rays 3 or 4 . . . . . Suborder GONORHYNCHOIDEI
  - 7a. Scales cycloid; gill openings not restricted; anterior ribs articulating in part with parapophyses wedged into pits in the centra; mouth terminal  
Superfamily CHANOIDEAE
  - 7b. Scales ctenoid; gill openings not restricted; anterior ribs articulating with strong lateral processes from the centra; mouth inferior  
Superfamily GONORHYNCHOIDEAE
  - 7c. Scales cycloid; gill openings little restricted; anterior ribs articulating directly with the centra; mouth superior . . . . . Superfamily PHRACTOLAEMOIDEAE
  - 7d. Scales cycloid; gill openings restricted; anterior ribs articulating directly with the centra; mouth inferior . . . . . Superfamily KNERIOIDEAE
  - 7e. No scales; gill openings restricted; mouth inferior . . . . . Superfamily CROMERIOIDEAE
  - 4b. No lower intermuscular bones; two rows of photophores along lower sides; posterior neural and hemal spines without antero-posteriorly expanded blades; no proethmoids . . . . . Suborder STOMIATOIDEI

- 8a. Premaxillary without anterior expansion; maxillary with two supramaxillaries; gill arches with gill rakers . . . . . Superfamily GONOSTOMOIDEAE
- 8b. Premaxillary with a strong anterior expansion extending upward over the ethmoid; maxillary without supramaxillaries; gill arches without normal gill rakers.
- 9a. Supracleithrum absent . . . . . Superfamily STOMIATOIDEAE
- 9b. Supracleithrum present . . . . . Superfamily ASTRONESTHOIDEAE
- 4c. No lower intermuscular bones; no photophores; posterior neural and hemal spines with antero-posteriorly expanded blades (except in *Lovettia* and the Salangidae); proethmoids sometimes present . . . . . Suborder SALMONOIDEI
- 10a. Two upturned postterminal vertebral centra . . . . . Superfamily SALMONOIDEAE
- 10b. Not more than one upturned postterminal vertebral centrum.
- 11a. Oceanic fishes with small pelagic eggs. . . . . Superfamily ARGENTINOIDEAE.
- 11b. Inshore or freshwater fishes with large, demersal eggs . . . . . Superfamily OSMEROIDEAE
- 4d. No lower intermuscular bones, photophores, or antero-posteriorly expanded blades on the posterior neural and hemal spines; paired proethmoids present  
Suborder ESOCOIDEI
- 12a. Snout not greatly produced; no canine teeth.
- 13a. Scapula, coracoid, and pectoral radials not ossified . . . . . Superfamily DALLIOIDEAE
- 13b. Scapula, coracoid, and pectoral radials ossified . . . . . Superfamily UMBROIDEAE
- 12b. Snout greatly produced; canine teeth present. . . . . Superfamily ESOCOIDEAE
- 1b. Parasphenoid terminating well short of the posterior end of the basioccipital. Parasphenoid sometimes with lateral processes for articulation with the mesopterygoid; anterior ribs either articulating directly with centra or with strong parapophyses that are fused to the centra; branched caudal rays 16 or fewer  
Division OSTEOGLOSSI
- 14a. Three or four uroneurals in the caudal skeleton; no parasphenoid facet for articulation with the mesopterygoid; nasals small; symplectic a normal, splint-like bone; basisphenoid absent; top of skull without longitudinal ridges.  
Superfamily HIODONTOIDEAE.
- 14b. No separate uroneurals nor parasphenoid facet; nasals enlarged; symplectic expanded; basisphenoid present; top of skull with longitudinal ridges  
Superfamily NOTOPTEROIDEAE
- 14c. No separate uroneurals; parasphenoid facets present; nasals enlarged; basisphenoid present; top of skull rugose but without longitudinal ridges  
Superfamily OSTEOGLOSSOIDEAE

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